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Variation and Extent of Eccentric Preformative Molt in Field Sparrows

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ABSTRACT

We examined 158 hatching year Field Sparrows (Spizella pusilla) to assess wing feather replacement during the preformative molt from 2010-2012 in Maryland. We recorded all replaced feathers within the primary, secondary and primary covert feather tracts. The number and order of feather replacement was highly variable among individuals. We found 22% of birds replaced at least one primary covert and 2.5% replaced all the primary coverts. At least one feather in both the primary and secondary feather tracts were replaced in 65% of individuals. Only secondaries were replaced in 20% of birds, and of these birds, 88% replaced one to three tertials only. Field Sparrows showed three molt sequences; typical, eccentric and both. Eight percent of individuals showed both patterns, making Field Sparrows only the seventh North American species documented to molt in this way. Overall, 72% of the birds in our study showed eccentric replacement patterns during the preformative molt. Our observations are the first to quantify primary covert replacement during the eccentric preformative molt in Field Sparrows.

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INTRODUCTION

The term eccentric was first used by European ringers (e.g., Jenni and Winkler 1994) to describe wing feather replacement patterns that vary in number and order of some (but not all) primaries and secondaries. The definition of eccentric feather replacement was then refined by Pyle (1997, Pyle et al 1997) and others to pertain specifically to primary molt that begins in the middle of the tract and proceeds distally. Eccentric feather replacement has been documented in 46 North American passerines; of these, 38 species showed eccentric replacement patterns of the outer primaries, inner secondaries and outer primary coverts during the preformative (first prebasic) molt only (Pyle 1997, Pyle et al 1997). In contrast, the majority of passerines follow the typical replacement pattern in which feather replacement commences with the innermost primary and proceeds distally, and the secondaries (after replacement of the tertials) with the outermost and proceeds proximally (Pyle 1997, Pyle et al 1997). Only six passerine species have been documented showing both eccentric molt sequence and typical molt sequence concurrently and only one of those species is in the Emberizidae family (Pyle 1997, Pyle et al 1997). The species previously documented as having both patterns are Carolina Wren, Song Sparrow, Lazuli Bunting, Varied Bunting, Blue Grosbeak, and House Finch (Pyle 1997, Pyle et al 1997). Pyle (1997, Pyle et al 1997) found five species of Emberizidae that replace one to four primaries coverts during the preformative molt; of these species, none were in the genus *Spizella*. Prior to this study, Willoughby (1991) was the only researcher to report primary covert replacement in Field Sparrows. Here we provide quantitative details on extent of primary, secondary and primary covert replacement during the preformative molt for Field Sparrows on the eastern shore of Maryland.

METHODS

From 2010 to 2012, we examined wing-feather molt in the primary coverts, primaries and secondaries on 158 hatching year (HY) and second year (SY) Field Sparrows. Birds were captured and processed at two locations less than a mile (1609.3m) apart run by the Chester River Field Research Station (39.23 N, 76.00 W): a restored grassland and a long-term migratory banding station, Foreman's Branch Bird Observatory. The number of replaced feathers was recorded for the right wing on all birds and for both wings ($n=70$) when time allowed. The difference between juvenal and formative feathers was determined by color, wear, sheen, shape and size. Retained juvenal remiges and coverts were always lighter and duller brown, more worn, and often shorter. In contrast, formative feathers were a darker and shinier brown (especially the feather shaft), showed less wear, and were longer and more rounded. Though subtle, the differences are readily discernible to the trained eye. In addition, we used eye color, rectrix shape and, as needed, skull ossification to confirm ages. These characters reliably separate HY and SY birds from after-hatching-year and after-second-year birds through the fall and into the following summer (their second calendar year).

Primaries (p1-p9) and primary coverts (pp cov 1-8) were numbered distally (innermost to outermost) and secondaries (s1-9) were numbered proximally (outermost to innermost). Only primary coverts 1 - 8 were examined during this study; we did not include molt status on primary covert 9 due to its small size relative to the adjacent coverts. Data are presented for both wings on 70 individuals to show whether the eccentric preformative molt was or was not symmetrical.

RESULTS

The preformative molt in Field Sparrows was highly variable and commonly eccentric. On most birds we detected incomplete molt patterns in the primaries, secondaries and/or the primary coverts. Eccentric replacement patterns showed on 115

individuals (72%). Variation in the number of feathers replaced ranged from zero feathers in 12% (20) of individuals to all feathers in one individual. Twenty-two percent (35) replaced at least one primary covert (range 1-8) and 2.5% (4) replaced eight. On the right wing, the average number of primary coverts replaced was 3.6. The number of primary coverts replaced increased significantly as more primaries were replaced (Figure 2, linear regression, $y = 0.74x - 1.89$, $F = 11.09$, $P < 0.01$). The average number of primaries replaced on the right wing was 5.8 and the average number of secondaries replaced was 4.0. Of the examined HYs, 21% (33) replaced only secondaries and 88% (29 out of 33) of those replaced only tertials (range 1-3). All birds that had eccentric replacement patterns also replaced all three tertials, except for two individuals. In the excepted cases, one bird replaced only secondary 9 and the other replaced secondaries 8 and 9.

Of the 158 birds for which molt data was recorded, 57.6% (91) showed eccentric molt patterns, 30.4% (48) had no preformative molt or only molted the tertials, 8.2% (13) exhibited both typical and eccentric patterns. Five (3.2%) had a typical molt sequence in the primaries and secondaries (starting at p1 and s1), but also molted primary coverts, though not starting at the first primary covert. Thus, while the primaries and secondaries showed the typical pattern, the primary coverts showed an eccentric replacement pattern. One individual (0.6%) had molted all primary coverts, primaries and secondaries completely, with the only juvenal retained feathers being the outer two greater coverts and the carpal covert. This bird was aged by a combination of retained coverts and eye color.

In all cases where molt was examined, primary coverts and primaries were always molted distally and secondaries always were molted proximally (excluding the tertials). This was also true for the 13 individuals that showed both the typical and eccentric molt patterns concurrently. No individual with eccentric replacement patterns had retained outer primaries.

We examined molt patterns on both wings of 70 individuals. Of these birds, 61.4% (43) had symmetric replacement patterns on both wings, while 38.6% (27) showed asymmetrical feather replacement between wings. Seventy percent (19) asymmetric individuals had only one feather different between wings, 15% (4) had two feathers, 7% (2) had three feathers and 4% (1) of birds had each four and five feathers that differed.

Only two individuals were caught while actively replacing their remiges, including their primary coverts. Fig. 1 is included to illustrate that primary covert feather replacement is not necessarily linked

to the corresponding primary feather. In addition, these two birds demonstrate that the primary coverts are molted simultaneously with the ongoing eccentric preformative molt and are also molted distally, though from different starting points than the primaries. Primary covert molt was initiated from varying number of feathers (pp cov 1-8), but was almost always from a single starting point with the exception of three individuals. Like the primary coverts, the primary molt was most often initiated from a variable single starting point. Molt of secondaries can proceed from either two different initiation points (from s1 through s6) or from only one (s6).

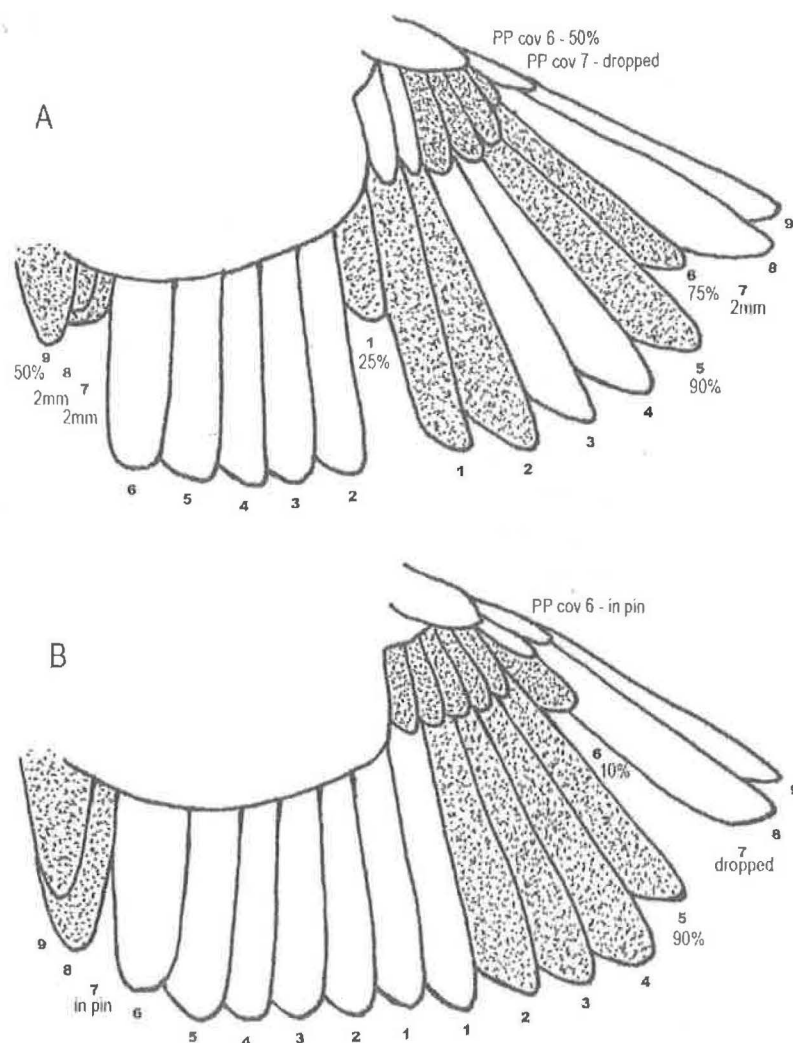


Fig. 1. Illustrations of two hatching year Field Sparrows undergoing eccentric preformative wing feather molt. Both birds were caught in September; (A) on 13 Sep 2011 and (B) on 9 Sep 2011. Shaded feathers are replaced formative feathers. Bird (A) is undergoing a typical molt and an eccentric molt concurrently

DISCUSSION

Studies on Field Sparrow molt date back to Dwight (1900) and Chapman (1910). Knowledge of Field Sparrow molt was later refined by Pyle et al. (1997). Willoughby (1989 and 1991) described the eccentric replacement patterns during the preformative (1st prebasic) molt and was the first to report primary covert replacement. Working with a smaller sample, Willoughby (1991) found one individual bird, 20% (n=5), had replaced primary coverts eight and nine on the left wing only during the preformative molt; our study with a much larger sample size found a similar percentage of individuals, 22% (n=158) had replaced at least one primary covert. Distribution of replaced feathers during the preformative molt ranged from 0 to 8 for the primary coverts, 0 to 9 for the primaries and 0 to 9 for the secondaries.

Field Sparrows in our sample showed three molt sequences; typical, eccentric and both. Of particular interest are the birds exhibiting both typical and eccentric patterns together. Field Sparrows are only the seventh documented species to show both molt patterns concurrently (Pyle 1997a, 1997b). Birds in our study exhibiting both molt sequences fall into two categories: birds with typical molt sequences in the primaries and secondaries, but eccentric molt patterns in the primary coverts, or birds that have both typical and eccentric molt patterns within one feather tract (see Fig. 1A). Five individuals replaced all primaries and secondaries, but only their outer primary coverts (range 4-6) in an eccentric sequence (not starting at pp cov1), with three of the five skipping one or two consecutive feathers. Thirteen individuals showed both eccentric and typical molt patterns in either their primaries or secondaries. Only one individual had both patterns in the primaries starting at primary 1 (see Fig. 1A), a second individual molted primary 5, skipped p6-7 and replaced p8-9. All 13 of these individuals had both patterns in their secondaries, 10 individuals had molt initiation at secondary one and a second initiation point starting between secondary four to seven. Three individuals had initiation points at secondary two or four and at secondary seven. It

could be argued that the one individual molting p5 and p8 and 9, and the three individuals molting s2 or s4 and s7 are actually showing two eccentric molt sequences within one feather tract, since starting molt from anywhere other than p1 or s1 would not be considered typical.

Reasons for replacing primaries and secondaries during the preformative molt are well established. Bright, harsh sunlight degrades feathers faster than do shaded environments. Thus, replacing juvenal secondaries with formative feathers that are structurally stronger (Dwight 1900, Jenni and Winkler 1994, Pyle 1998) and more durable would better protect the rest of the wing from sun exposure. Likewise birds that spend most of their time in thick vegetation abrade their weaker juvenal outer primaries faster than formative feathers (Willoughby 1991). Tables 1 and 2 demonstrate that outer primary coverts and primaries and inner secondaries are replaced at a higher rate than less exposed feathers. Field Sparrows spend their entire life cycle in exposed sunlit habitats, foraging in open vegetation dominated by grass and/or thick scrubby areas (Carey et al. 1994). Thus replacement of these flight feathers is essential because retained poor quality juvenal feathers would have to last until after the following breeding season, up to ten months later.

The reason for eccentric molts in Field Sparrows and other species that share similar habitats seems straight forward; however, reasons for incomplete replacement of the primary coverts are less clear. Primary coverts cover the base of the primary shafts where they are anchored in the wing. Protecting this area and creating a smooth surface between the leading edge of the wing and the primaries improves flight dynamics (Dwight 1900). In addition to replacing outer primary coverts that are degraded by the sun, another possible reason for molting primary coverts during the preformative molt could be to replace these weaker juvenal feathers that are less efficient at maintaining a smooth wing surface, compared with the stronger formative feathers. Formative feathers would break down more slowly and continue to maintain a smooth intact wing surface through the following breeding season.

Table 1. Frequency and percent of primary coverts, primaries and secondaries replaced on the right wing during the preformative molt in Field Sparrows. Percentages refer to the number within the sample that molted the corresponding feather; e.g., 8.9% of birds replaced primary covert 6 during the preformative molt.

Right Wing Feather Replacement										
N=158		1	2	3	4	5	6	7	8	9
Primary Coverts	Frequency	5	6	6	6	13	14	23	24	-
	%	3.2	3.8	3.8	3.8	8.2	8.9	14.6	15.2	-
Primaries	Frequency	8	14	30	67	89	96	98	101	102
	%	5.1	8.9	19.0	42.4	56.3	60.8	62.0	63.9	64.6
Secondaries	Frequency	18	11	8	17	30	75	116	129	137
	%	11.4	7.0	5.1	10.8	19.0	47.5	73.4	81.6	86.7

Table 2. Frequency and percent of primary coverts, primaries and secondaries replaced on the left wing during the preformative molt in Field Sparrows.

Left Wing Feather Replacement										
N=87		1	2	3	4	5	6	7	8	9
Primary Coverts	Frequency	1	4	1	3	5	12	13	12	-
	%	1.1	4.6	1.1	3.4	5.7	13.8	14.9	13.8	-
Primaries	Frequency	4	8	17	36	42	48	49	51	51
	%	4.6	9.2	19.5	41.4	48.3	55.2	56.3	58.6	58.6
Secondaries	Frequency	7	4	6	10	22	37	55	61	66
	%	8.0	4.6	6.9	11.5	25.3	42.5	63.2	70.1	75.9

Gargallo (2013) demonstrated that European Goldfinch determine the extent of their partial post-juvenile molt, equivalent to the North American incomplete molt, with precision in advance or at the beginning of the molt. Extent of molt is governed by day length, with older birds replacing a greater number of feathers and later hatched birds molting fewer (Gargallo 2013). The number of primaries and primary coverts that Field Sparrows replaced varied between individuals. For those that replaced primaries or primary coverts, the outer feathers were always replaced, regardless of the initiation point. Field Sparrows, as European Goldfinches, appear to be determining the extent of the molt in advance based on hatch date or time remaining in the season and molting high priority feathers (Gargallo 2013).

Field Sparrows replaced a greater number of primary coverts as more primaries were replaced (Fig. 2). Birds that have a more extensive molt are making a decision to not only to replace additional primaries, but also primary coverts. Though these primary coverts are molted distally as are the primaries they are not necessarily linked to the corresponding replaced primary.

We encourage other banders to look for molt limits within the primary coverts of the Field Sparrows they handle. Many questions remain about the reasons for this additional molt and why there is so much variation. Is there geographic variation among populations of Field Sparrows with respect to primary covert molt?

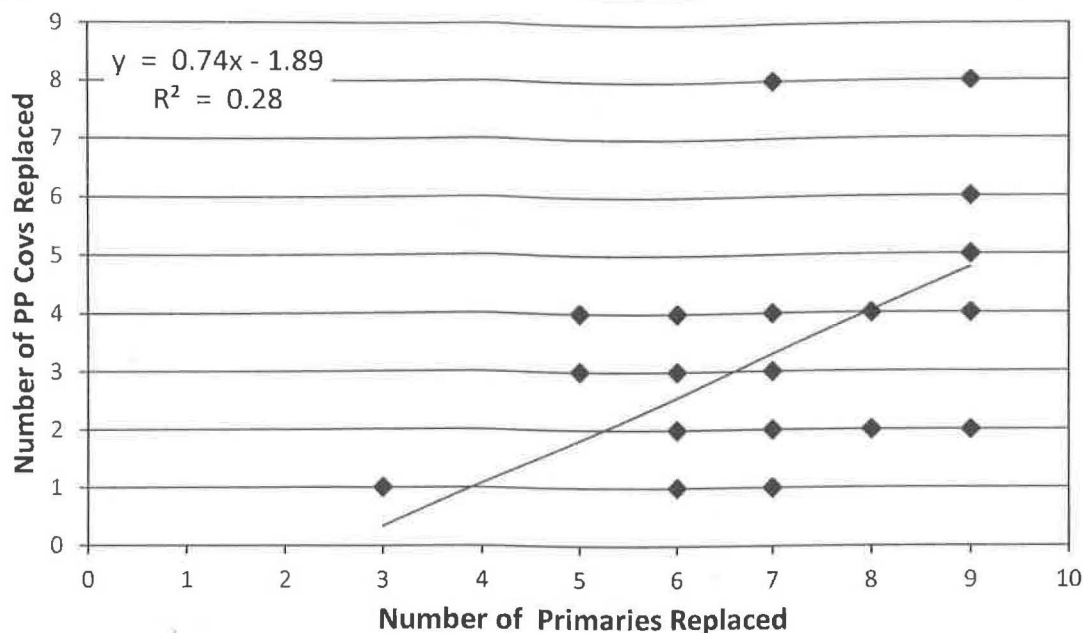


Fig. 2. In birds that replaced primary coverts, the number replaced increased significantly with the number of primaries replaced: $n = 30$, $F = 11.09$, $P = .002$. Possibly representing an anomaly, one individual replaced eight primary coverts and only seven primaries; birds showing eccentric molt patterns generally replace at least two fewer primary coverts than primaries (Pyle personal communication).

Are there differences between migratory populations and resident populations or perhaps between the sexes? Documenting primary covert replacement in other species that have incomplete eccentric preformative molts might help elucidate the function of and reason for this additional feather replacement.

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